

is required in the propagation of the electric response, and that the physico-chemical change producing the response is the only factor involved in the propagated nervous impulse.

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A Method of Analysing Galvanometer Records.

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CROONIAN LECTURE :—*Release of Function in the Nervous System.*

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It is a common experience that the manifestations of nervous disease may comprise both loss of function and some positive outburst of excessive activity. Thus, in many cases of hemiplegia, the paralysed limbs tend to be more or less rigid and the reflexes are greatly increased. This spasticity, although due to a destructive lesion, was attributed to "irritation"; the morbid agent, or the conditions it produced in the nervous system, were supposed to have an "irritative" effect upon the tissues, and this was expressed in the positive signs and symptoms.

But more than fifty years ago, Hughlings Jackson [11]* laid down the rule that destructive lesions never cause positive effects, but induce a negative condition, which permits positive symptoms to appear. This he applied to all morbid expressions of nervous activity; but his most striking instance was the motor condition in organic hemiplegia. He showed that it depended on two factors. First, there was loss of voluntary power, especially in the fingers, the parts most directly under cortical control; this was the negative

* Numbers in square brackets refer to List of References at end.

effect of the lesion. Secondly, the positive symptoms consisted of that massive overaction spoken of as "spasticity," the result of the unrestrained energy of lower centres. It was not due, as was commonly supposed, to "irritation," but to release of such centres from the control normally exercised over them by those on a higher functional level.

This doctrine, in its specific application to certain phenomena of hemiplegia, was widely accepted, especially in England; but it was not generally applied to the phenomena of nervous disease, and it is still the custom to attribute to "irritation" most of the excessive reactions produced by organic disease or injury.

All observers are agreed that the various centres of the nervous system form a hierarchy in which some exercise higher functions than the others; but the idea that an abnormal response may be an expression of the activity of these subordinate centres has not penetrated widely into neurological medicine. The phenomena of disease are thought to be purely adventitious; they are spoken of as "pathological," and are supposed to bear no relation, even remotely, to any mode of response which has previously existed in the individual or the race.

We believe, on the other hand, that in the gradual evolution of function, the reactions of the lower centres have been changed to suit fresh conditions. The more complex an organism, and the more efficiently it responds with discrimination to external forces, the greater will be the need for such readjustment. Older modes of response must be modified or suppressed; some are utilised in the newly acquired complex act, whilst others, under normal conditions, are prevented from playing a part. But wherever diminution or removal of a dominant group of functions leads to an excessive outburst of energy, the more primitive responses have not been abolished; for had they disappeared completely in the process of evolution, destruction of a higher centre would produce loss of function only, unaccompanied by signs of over-activity. Normally, they are suppressed because they would disturb the more discriminative responses of higher centres; but they still remain capable of revival under conditions demanding urgent and impulsive action.

Release of function, due to failure of higher centres to exercise normal control, can occur in two ways. Structural changes may so lower their capacity that they can no longer play a dominant part in some complex act, and suppress inappropriate manifestations from subordinate centres. In this case the morbid phenomena consist both of loss of function and over-action. This I shall speak of as "disintegration," for it involves the breaking up of an integrated series of responses.

Secondly, some reaction, normally dominated or suppressed, may break through owing either to the extreme* vehemence of the stimulus or to diminution of the controlling energy, due to causes other than organic destruction. Here the whole of the morbid manifestations consist of positive signs and symptoms unaccompanied by loss of function. This I shall call "escape from control."

1. *Disintegration.*

Sherrington's physiological work on the reflexes [16], and especially his explanation of decerebrate rigidity, gave an experimental proof of Jackson's law of release of function. If the cerebral hemispheres are removed, or better still, if the animal is decapitated through the mid-brain, all four limbs fall into a condition of postural rigidity, due to prolonged spasm of certain voluntary muscles. The head is lifted and the tail may be stiffly curved upwards. This attitude is essentially adapted to resist the force of gravity and, if the limbs are passively flexed by the experimenter, considerable resistance is encountered. The knee-jerk assumes a characteristic form; on tapping the tendon a quick extensor movement is produced, but the limb does not return to its original position. Removal of controlling influences from above permits these postural activities of lower centres to manifest themselves unchecked, for the cortex is concerned mainly with the initiation or inhibition or movement and not with posture.

When the spinal cord is divided in man, or so gravely injured that conduction is destroyed, the lower extremities lie flaccid and atonic on the bed, in any position into which they may be placed. The urine is retained and the patient has no power of evacuating his bowels. All deep reflexes are abolished, and scratching the sole of the foot may either produce no movement of the toes or one that is feebly downwards; the receptive field for this reflex is restricted to the sole or even to the outer portion of the under surface of the foot.

Should the patient be young and strong, particularly if he remains free from cystitis, bed-sores, or fever, the deep reflexes reappear as the period of spinal shock passes away. The ankle jerk and then the knee jerk can be obtained; gradually the plantar reflex begins to assume a form characterised by an upward movement of the great toe. The field from which it can be evoked enlarges, and finally, in successful cases, the spinal cord becomes so excitable that stimulation anywhere below the level of the lesion may be followed by a characteristic upward movement of the toes. But this is a small portion only of the movements produced by nocuous stimulation; the ankle is dorsiflexed and the lower extremity bent both at knee and hip; not infrequently the abdominal wall contracts and every flexor muscle

below the lesion may participate in an energetic withdrawal of the foot from harm.

Still more remarkable evidence of diffusion of afferent impulses within that part of the spinal cord which lies below the lesion is shown by the behaviour of the bladder and rectum. Not only can evacuation be facilitated by pricking the sole of the foot or by any manipulation which produces a flexor spasm, but passing fluid into the bladder or rectum may evoke an upward movement of the toe, accompanied by other flexor manifestations of the lower extremity ([9], p. 467, *et seq.* Riddoch [13]).

This condition has been spoken of as a "mass-reflex," because any afferent excitation below the level of the lesion is liable to produce motor effects not only in the parts normally thrown into action by such a stimulus, but also in organs that do not usually lie within the arc of its reflex influence. The bladder can be excited to action by stimulating the sole of the foot, and movements of the toes can be evoked by filling the bladder with fluid.

Removal of the influence of the higher centres from those of the spinal cord has led to a condition in which the outburst of energy, produced by appropriate stimulation, is not only excessive but unduly widespread. Judged, however, by the strength of the stimulus, there is nothing to show that the spinal centres have become more excitable; but they have been released from control and respond with a more massive and less discriminative reaction.

It has long been recognised that an apoplexy may be followed by painful sensations of extreme severity on the opposite half of the body. Largely owing to the researches of Dejerine and his co-workers (Dejerine and Egger [1], Dejerine and Roussy [2]), we now know that the lesion in such cases usually lies within the optic thalamus. Roussy ([14] and [15]), further elaborating these signs and symptoms, described a "syndrome thalamique"; five careful *post-mortem* examinations confirmed his diagnosis, and many others have since been reported which showed the truth of Dejerine's original generalisation (Long [12], Winkler and van Londen [20], Holmes and Head [10]).

The optic thalamus is one of the most intricate regions of the central nervous system and, since most pathological conditions in this situation do not produce selective destruction, the clinical picture presented by a thalamic lesion is usually extremely complex. But by a suitable choice of illustrative cases and by analysis of the symptoms they present, it is not difficult to discover the part played by this organ in sensation. (Head and Holmes [9], p. 551, *et seq.*)

First, it forms the receptive end-station for all sensory impulses. From this point they start on a fresh course to culminate in two centres, the cortex

cerebri and the essential organ of the thalamus itself, each of which subserves a complementary aspect of sensation. Any sensory loss which may be produced by a lesion of the optic thalamus differs in no way from that caused by interference with afferent impulses, either as they enter this organ, or as they pass to the cortex by way of the internal capsule. But to these familiar defects may be added another factor, a tendency to react excessively to all potentially affective stimuli. The prick of a pin, painful pressure, excessive heat and cold, all produce more distress than on the normal side. At the same time, pleasurable warmth may evoke an unusually vivid response, and general affective states induce a more profound reaction over the disordered half of the body.

It was customary in the past to explain the pains and discomfort, which occur under such conditions, as due to "irritation." The lesion was supposed to "irritate" some part of the sensory path in the region of the optic thalamus and thus to produce pains and "hyperalgesia." But this conventional hypothesis is insufficient to explain the facts observed during the clinical course of those cases.

In the large majority of instances, the lesion proved to be of vascular origin and consisted of a hæmorrhage or softening. Now, such disorders of the central nervous system usually arise more or less suddenly; provided the destruction is not progressive, they tend to produce the maximum loss of function at the time of, or shortly after, their onset. Subsequent progress on the part of the patient is always accompanied by a certain amount of recovery. But in this group of thalamic cases the pains and over-reaction come on as a rule during the period of restoration of function, frequently a considerable time after the "stroke" has occurred, and they usually last unaltered for years. Moreover, the response to pleasurable stimuli may also become excessive, a condition entirely incompatible with the existence of an irritative process capable of evoking pain and discomfort.

Here, again, a gross organic lesion is followed, not only by loss of function, but also by positive over-action. This is due to the release of the optic thalamus and neighbouring parts from the control normally exercised by the activity of the cortex cerebri. On the afferent side, the essential organ of the thalamus is the centre for pain, heat, cold, and other affective aspects of sensation. When, therefore, it is freed from the restraining influence of the cortex, every stimulus capable of acting on this centre produces an excessive effect on the abnormal half of the body. Disintegration with release of function and not "irritation" is the cause of thalamic over-reaction.

From the earliest days of our work on the afferent nervous system we recognised that, when the skin was deprived of certain aspects of sensibility,

the response to those which remained might become peculiarly vivid. Reaction to a prick was abnormal and excessive; the patient complained that it was more painful, although measurements showed that sensibility to this form of stimulation was not increased.

When such a nerve as the median or ulnar is divided, the extent of the insensibility to pricking is usually less than that of the anaesthesia to light touch (see figs. 2 and 3). Some fourteen days or more after the injury, this intermediate zone begins to behave in a peculiar manner. If the point of a pin is dragged across the skin from normal to affected parts, it is said to be "more painful" or to "hurt more" as it passes over the portion of the palm sensitive to pricking, but not to the lighter forms of tactile stimulation. This would usually be spoken of as "hyperalgesia"; but measurements have shown that the threshold is raised to cutaneous painful stimuli, and that, although the response is excessive, this area is in reality one of diminished sensibility.

The phenomena exhibited by a part of the skin, sensitive to pain, heat and cold, but deprived of some of the higher elements of sensibility, could be worked out in greater detail during the course of the experiment on my arm. Within a little over six weeks, after division and reunion of my radial and external cutaneous nerves, sensibility began to return; seven months after the operation, the back of the hand was sensitive to pain, to cold, to heat and to any form of contact which moved the hairs. But the sensation experienced was peculiar and quite unlike any reaction from normal parts; for, although less easily evoked, it was unduly vivid. The pain of a prick was intolerable; cold was said to be colder, and a suitable warm stimulus produced a more actively pleasant effect than over the normal skin; during this stage of recovery a high threshold was associated with a brisker response ([9], p. 258, *et seq.*).

The sensation aroused within the affected area had certain other peculiar characteristics. It radiated widely and was not confined to the neighbourhood of the stimulated spot. Portions of the affected area seemed to be linked up together, so that stimulation of the one evoked a sensation of the same specific quality referred to the other. Thus, brushing the hairs, pricking, or the application of heat and cold to the neighbourhood of the index knuckle, caused a diffuse outburst of the appropriate sensation over the dorsal aspect of the thumb. Moreover, the response was massive, diffuse, and bore little relation to the measured strength of the stimulus, provided it was effective ([9], p. 297).

Trotter and Davies ([18], p. 121), who divided seven nerve trunks in different parts of their bodies, write as follows of these peculiar manifestations:—"In addition to their directly practical importance, intensification

(over-reaction) and peripheral reference are matters of great theoretical interest. To the subject of them they present a series of sensations entirely new and entirely outside his previous sensory experience, and yet they are surprisingly definite and unmistakable. No one who has not experienced them can appreciate the intense vividness with which they present themselves to the subject; and the investigator with no direct knowledge of them is likely even to be wearied by the importance their brilliance makes them assume in the subject's mind."

It has long been known that certain minute spots in the normal skin are especially sensitive to heat, to cold and to pain, although there was reason to believe that they were not the cause of all its sensory functions (Blix, Donaldson, von Frey). We were able to show that this punctate mechanism was responsible for the peculiar mode of reaction present during the first stage of recovery. For, whenever a part of the affected area became sensitive to heat, to cold, or to pain, one or more of these specific spots were discovered within it. At this stage, sensibility to contact was due solely to end-organs at the base of the hairs, and, if my hand was carefully shaved, I no longer responded to cotton-wool moved lightly over the surface.

All the organs of this punctate mechanism possess certain characteristics in common. They regain their function with great rapidity after the peripheral nerve has been successfully united and, for many months, the form assumed by the reaction of the skin to contact, to pain, to heat and to cold, shows that they alone are responsible for any sensibility it may possess. The response to a stimulus capable of exciting one of these organs is not strictly graduated by its intensity, but is arranged more nearly on an "all or nothing" principle.* So long as the stimulus is effective, it matters little how cold or how hot it may be; organs of this class indicate its quality, not its intensity.

A natural consequence of this mode of reaction is the overwhelming importance of the extent of surface covered by the stimulus rather than its intensity. For it is obvious that, if one cold-spot can be excited to vigorous

* In the protopathic response there is undoubtedly a "more or less-ness," which is of the same nature as that denoted by the term intensity; it is not, therefore, strictly an "all or nothing" reaction. But variations in the intensity of the stimulus are of less importance to the sensation evoked than the extent of surface or number of end-organs it affects. So much is this the case that in the experiments on my hand, a cold object covering several cold spots, but of higher temperature, caused a colder sensation than an ice-cold rod applied to one spot only. Weber's law, and other expressions of exact quantitative relations between stimulus and sensation, do not hold for states of protopathic sensibility ([9] pp 306-311). It is the business, therefore, of the central nervous system to replace these impulsive responses by more discriminative sensations.

activity by 20° C., a stimulus at the same temperature, sufficiently extensive to cover many cold spots, will seem to be colder, although in reality its intensity is the same. Thus, whenever sensation depends solely on the response of this class of end-organs, the extent of the stimulus is of greater importance than its intensity.

A peculiarity of this reaction, from any part of the skin innervated by this punctate system only, is the diffuseness and wide radiation of the sensation evoked. When a hair-clad part, such as the back of the hand, is stroked with cotton-wool, an intense "tingling" and "itching" is produced over widely remote parts of the affected area. This disappears when the skin is shaved, and is due to movement of the shafts of the hairs; it is not a function of the skin as a whole. In the same way, each effective hot, cold or painful stimulus produces its specific sensation, which is referred to the same remote parts of the affected area, irrespective of any difference in quality ([9], p. 302).

Thus an area, obviously defective in sensibility, is found to respond with extraordinary vividness and with a widespread massive sensory reaction. These manifestations grow steadily stronger throughout the first stage of recovery, with the gradual return of sensibility to pain and the increasing number of heat- and cold-spots.

Throughout this period the more discriminative aspects of sensation have been absent or very defective. But as soon as they begin to return, the mode of reaction changes. The diffused sensations give place to a more strictly localised response; radiation no longer occurs into remote parts of the affected area. At the same time, the power returns of distinguishing two compass-points, applied simultaneously. This is essentially an ability to recognise objects in two dimensional space, and it is this discriminative power which checks and controls the diffuse character of the more primitive method of response. The impulsive reaction of the heat- and cold-spots gives place to one graduated more closely according to the intensity of the stimulus, as the affected part becomes sensitive to temperatures which lie in the middle of the scale (27° to 38° C.).

Another remarkable change, due to the restoration of the more discriminative aspects of sensibility, is shown in the return of adaptation to different temperatures. Under normal conditions, if the hand has been exposed for some time to warmth, a stimulus at 29° C. may seem to be "cool," whilst, conversely, if it has been adapted to cold, the same object may appear to be "warm." So long as the skin is actively innervated solely by the punctate sensory mechanism, no such adaptation is possible within normal limits, and any effective thermal stimulus appears to be hot

or cold, irrespective of the temperature to which the part has been previously exposed ([9], p. 292).

How completely these changes in the form of the response are due to recovery of control by a dominant system over the activity of one or more primitive functions was shown by the behaviour of my hand when exposed to the injurious effects of cold. The higher forms of sensibility are liable to be unfavourably affected by the general action of external cold, especially before they have been completely restored. At a time when almost the whole of the back of my hand had so far recovered that referred sensation could no longer be produced, the palm was placed upon ice; radiation and reference reappeared as vividly as of old, and the hand was thrown back for a time into its previous condition. The newly recovered activity of the high-grade system was disturbed by the cold, and impulses from the more primitive mechanism, previously inhibited, now passed on to reach consciousness uncontrolled.

This control may be exerted even by impulses from the healthy skin in the neighbourhood, if adjacent normal and abnormal parts are stimulated simultaneously. When a cold tube was placed so that it fell just within that part of the dorsum of the hand which was in a purely protopathic condition, a vivid referred sensation was always experienced in the thumb. But when the base of the tube fell partly within the affected area and partly over the adjacent normal skin, reference to the thumb was abolished. The only sensation produced was one of coldness around that part of the back of the hand in contact with the tube.

If this massive and ill-defined response were due to structural changes inherent in the act of recovery, it is difficult to see why it is not always present, whenever nerve fibres conducting painful and thermal impulses undergo regeneration. Occasionally it happens, by a fortunate chance, that after division of cutaneous nerves some part of the denervated area retains its discriminative sensibility to the lighter forms of tactile stimuli, though insensitive to prick, heat, and cold. With the restoration of these aspects of sensation, pain-, heat-, and cold-spots make their appearance; but under such conditions, the response is not unduly vivid, diffuse, or referred to remote parts. Recovery within an area already endowed with the more discriminative forms of sensibility is not accompanied by the phenomena we have attributed to loss of control ([9], p. 287). If over-reaction were due to irritation of "pain-fibres" in the course of regeneration, it should be independent of the coincident presence or absence of other sensory activities; but this is not the case.

Moreover, it is important to remember that this over-reaction is limited to

areas which have lost the more discriminative aspects of tactile sensibility. The cutaneous fibres of the ulnar nerve, which conduct painful impressions, extend into the "median area" on the radial half of the palm. In a similar manner, a varying portion of the so-called "ulnar area" is innervated by fibres from the median. The supply of these two nerves overlaps con-

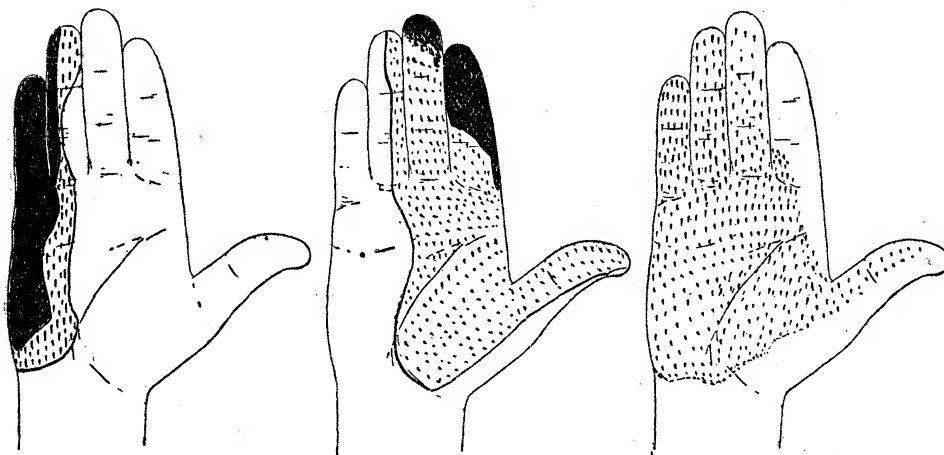


FIG. 1.

FIG. 2.

FIG. 3.

FIG. 1.—To show the effect produced by surgical division of the ulnar nerve. (From the same patient as fig. 3; the tenderness has disappeared.) The black area corresponds to the complete cutaneous analgesia. The dotted area represents the parts in a condition of protopathic sensibility; the surface was insensitive to the lighter degrees of contact, such as cotton-wool, and two points of the compasses could not be discriminated within normal limits. If a pin was dragged lightly across the palm from normal to abnormal parts it was said to "hurt more" when it passed to the ulnar side of this border.

FIG. 2.—To show the extent of the changes in cutaneous sensibility which may follow division of the median nerve. The black area corresponds to the complete cutaneous analgesia. An example has been chosen where the extent of this total loss was comparatively small. The dotted area represents the parts in a condition of protopathic sensibility; this does not extend beyond the limits of the loss to the lighter degrees of tactile stimulation.

FIG. 3.—To show the extent of the superficial tenderness on the palmar aspect of the hand, due to irritation of the ulnar nerve caused by a bullet wound of the forearm (Head and Sherren [9], p. 210, *et seq.*). The limits of this tenderness could not be defined exactly as it merged into parts that responded normally to the point of a pin dragged lightly across the surface. All tenderness disappeared after division of ulnar nerve (*cf.* fig. 1).

siderably as far as painful sensibility is concerned. But the extent of the over-reaction, which may follow division of one or other of these peripheral nerves, is strictly limited to the borders of loss to the lighter degrees of tactile stimulation; it does not spread beyond them on to those parts of the

palm which we know to be supplied with "pain-fibres" from the injured trunk.

When, however, excessive reaction to prick is really due to irritation of a peripheral nerve, as in some cases of causalgia (fig. 3), the extent of the cutaneous tenderness is not limited by the loss of tactile sensibility, which is often slight; it spreads across the palm on to all those portions innervated from the injured nerve, and can be abolished by transecting it completely ([9], pp. 160 and 212).

I have attributed these morbid conditions, where gross loss of function is accompanied by unduly vivid reactions, to removal of some influence from above on the activities of lower levels of the nervous system; this doctrine has been widely opposed. Many hold that, when a complex function is broken up, the resultant positive manifestations are purely adventitious, and throw no light on the inherent reactions of the lower centres. Morbid changes lead to disordered action, of which "irritation" and excessive responses form an integral part.

But there can be no doubt that the postural rigidity of the decerebrate animal and the spasticity in hemiplegia express the activity of centres, which have remained unaffected by cerebral destruction. In the same way, the excessive responses to affective stimuli, which appear when the optic thalamus has been released from cortical control, and the mass-reflex obtained from the lower end of the spinal cord demonstrate the mode of reaction of these centres, when they are no longer dominated from above.

I have included in the same category the condition we have called "protopathic" sensibility,* which may appear after complete division of

* The terms "protopathic" and "epicritic" are applicable solely to forms of cutaneous sensibility, revealed by destructive lesions of the peripheral nervous system, and should not be employed for the products of dissociation at higher levels. All afferent impulses undergo regrouping, according to their potential sensory qualities, at the first synaptic junction. For instance, those due to painful impressions from the surface of the body are combined with equivalent impulses, produced by excessive pressure on deep end-organs, and travel up the same specific tract as far as the optic thalamus. In the same way the products of thermal stimulation, arising in the "protopathic" or "epicritic" mechanism of the skin, are sorted and re-grouped according to their power of arousing sensations of heat or cold. The optic thalamus forms the centre for qualitative and affective modes of sensation, whilst the so-called "sensory" cortex is occupied with its spacial and discriminative aspects. When the thalamus is freed from control, the abnormal half of the body reacts excessively to stimuli capable of evoking a response, whether pleasant or unpleasant, and in this way resembles a part in a condition of protopathic sensibility. But thalamic over-action is produced by the disintegration of a highly complex group of sensory functions, whilst protopathic sensibility is due to the uncontrolled action on normal centres of a set of impulses, heavily charged with feeling-tone and capable of inducing impulsive reactions.

a peripheral nerve in parts of the affected area which remain sensitive to pricking, but are anaesthetic to light contacts; it is also specially evident during the first stage of functional recovery under identical conditions of sensory dissociation. For in such circumstances impulses arising in the punctate afferent mechanism can exercise their influence on the central nervous system, unchecked by the more discriminative impressions; these are either absent or have not yet been fully restored. Whatever explanation is given for such abnormal forms of sensation, there can be no doubt that in their vividness and indiscriminative nature they represent some want of higher control.

All these examples of over-action, associated with gross loss of function, show certain primitive characteristics. They are not fortuitous perversions of a normal function, as some have contended, but reveal to a certain degree the mode of action of the lower centres before they were dominated from above. The reaction is massive and exceeds any normal response, both in vividness and extent; it is stereotyped, predetermined, and the same manifestations can be evoked from an abnormally wide receptive field. Moreover, it depends less upon the intensity of the excitation than on the amount of surface occupied by the stimulus, provided it is effective.

Thus, when a portion of the spinal cord is completely cut off from higher control, scratching the sole of the foot, or indeed any part below the level of the lesion, may produce spasmodic movements of the whole lower extremity and even of the abdomen. But this is not the only effect; bladder and rectum can be excited to evacuate their contents prematurely, and a profuse outburst of sweating be evoked by any nocuous stimulation. With the return of signs indicating that the higher centres again exert their influence on the lower end of the spinal cord, this want of differentiation ceases; scratching the sole of the foot no longer produces an effect upon the bladder and rectum, and the form assumed by the muscular response again begins to depend upon the situation and nature of the stimulus.

In the same way, on the afferent side, any effective stimulation of a protopathic area causes a vivid diffuse sensation, not uncommonly referred to remote parts at a distance from the place to which it is applied. The "more or less-ness" of the response is determined to a greater degree by the extent of the stimulus than by its intensity. The end-organs of the punctate system in the skin act as a warning mechanism; any form of excitation capable of producing a sensation leads to a highly impulsive but feebly discriminative reaction.

The abnormal vividness of a protopathic response applies not only to

painful but also to all potentially unpleasant stimuli ; the itching, produced by brushing the hairs of my hand, was more intolerable than any normal sensation. Pleasurable stimuli also evoke an excessive response, and the pleasure which accompanies moderate excitation of the heat-spots far exceeds that obtained from general stimulation of the normal skin with the same temperature. This exaggeration of the effect produced by potentially pleasurable stimuli forms a prominent feature in some cases of thalamic over-action, and has not been dealt with adequately by any of our critics. It cannot be explained by "irritation," nor is it a fortuitous perversion of some normal function. On the other hand, it falls into line with all the other phenomena we have attributed to loss of control.

Integration is the main business of the central nervous system, and within it the diverse effects produced on the living organism by external forces are sorted, combined and inhibited. Should the functions, which have been disturbed by an organic lesion, belong to the same level as those which are unaffected, the loss of one group has no material effect on the other ; there is none of that over-action so common, when dominant centres are destroyed. When the lesion is situated in the lateral columns of the spinal cord, sensibility to heat and to cold may be disturbed independently ; but isolated anaesthesia to heat over a certain part of the body is not accompanied by over-reaction to cold or *vice versa*. At this point in their course through the nervous system, the impulses underlying sensations of heat and cold have already undergone qualitative integration ; they run side by side in separate tracts and can be disturbed independently. Here they are equipollent ; no one sensory activity is dominated by the other, and structural changes produce loss of sensation unaccompanied by excessive responses.

If, however, the factor eliminated by the lesion has exercised some control over the functions which still remain intact, phenomena may appear which were inhibited under normal conditions. Suppose half the scholars are absent from a class, the sum total of its vital energy is diminished, but discipline is maintained unimpaired ; absence of the master, on the other hand, leads inevitably to disorder.

But it would be wrong to suppose that removal of a dominant mechanism reveals the reactions of a phylogenetically older organ in all their primitive simplicity. The integrative activity of the higher centres has profoundly modified the functions of those below them in the neural hierarchy ; some have been caught up to take part in the new complex, whilst others are held in check or inhibited. Thus, the reactions obtained under favourable conditions from the divided spinal cord in man are more specifically flexor than in the dog or cat. For in the lower animals the specialisation of function is less

complete and, when disintegration occurs, the separated spinal cord still retains certain functions which in man have mostly been assumed by higher centres. No flexor response is so free from postural characters as that which can be obtained from the lower portion of the human spinal cord after complete division. In the same way, the reactions of the optic thalamus in man, freed from cortical control, are an almost perfect expression of the non-discriminative aspects of sensation.

2. Escape from Control.

So far the phenomena I have described were due to disintegration of a complex function, normally carried out by the co-ordinated activity of centres at different levels of the nervous hierarchy. Before two such centres can work harmoniously, their various activities must be integrated, and during this process some impulses are inhibited, whilst others are facilitated. Of two antagonistic reflexes one becomes dominant, whilst the other is suppressed, according to circumstances, which are often more dependent on past events than on the immediate character of the stimulus. The issue of a conflict between opposing impulses is not inevitable; it is always possible for an unexpected or "abnormal" reaction to make its appearance, owing to some change in functional balance (Sherrington [16], p. 135).

The following experiment shows how completely one group of afferent impulses may inhibit another under perfectly normal conditions. On carefully exploring the back of the hand two or more cold-spots can usually be discovered in close proximity to one another. Stimulate any one of them by means of a metal rod, with a blunt end of not more than 1 mm. in diameter, heated to about 45° C.; the sensation will be one of coldness, as if the rod had been dipped in cold water. This is the familiar phenomenon of "paradox cold." Take a flat-bottomed metal tube containing water at about 45° C., of such a size that it will cover several cold-spots together with the skin around them. Lay this on the hand and you will experience a pure sensation of heat; and yet observation teaches us that this temperature is capable of evoking a sensation of cold, if it is applied to each of the cold-spots individually. Under normal conditions, however, the effect produced by stimulating the cold-spots is dominated, before it can affect consciousness, by the coincident impulses due to action of the same external physical agent on the end-organs which respond to heat.

The older investigators believed that an impulse, once started in specific end-organs, travelled unchanged to the highest receptive centres, to evoke a response corresponding in quality and degree to the sensory attributes of the physical stimulus. Such a theory ignores the fact that 45° C. is an effective

stimulus to the heat-, the cold-, and the pain-spots, and yet, under normal conditions, produces a sensation of pleasant warmth only. Between the impact of a physical stimulus on the peripheral end-organs and the simplest changes it evokes in consciousness lie the various phases of physiological integration. We are accustomed to think of the external stimuli we employ in scientific investigation as if they caused unitary effects; but in reality they produce a multitude of diverse physiological reactions. The simplest physical condition acting on the peripheral nervous system may produce afferent impulses which are incompatible from the point of view of sensation. But the stimuli of daily life are not simple; they are extremely complex and give rise to a multitude of diverse impressions. These must be sorted and regrouped; some are facilitated, others are suppressed before the final sum is presented to consciousness. Many afferent impulses remain on the physiological level and never form the basis of consciousness; they are destined to control reflex activity or to co-ordinate movements of the body and limbs.

We must not forget that the larger number of afferent impulses, arising in peripheral end-organs, do not travel the whole length of the central nervous system. Their essential task is to excite and co-ordinate reflex action without of necessity giving rise to sensation, and the earlier phases of integration are undoubtedly adapted to this end. Such co-ordination could not occur if there was no qualitative selection of afferent impulses at the receptive junctions of the various reflex arcs. The main function of the intramedullary receptors is to increase the excitability of the reflex arc for one kind of stimulation and to diminish it for all others. This ensures a selective response to the complex results of peripheral excitation, and at the same time precludes many afferent impulses from influencing consciousness. Thus, for example, visceral insensibility is a function of the specific reaction of receptors, and not the consequence of an absence of afferent impulses.

Each specific group of receptive organs within the central nervous system works on the same principles; it accepts those elements of a massive reaction which can excite it to activity and rejects those to which it cannot respond. At the same time, there is evidence to show that the synaptic junctions are subject to those refractory states and phases of heightened activity characteristic of all neural action.

These three processes, selection of certain impulses, rejection of others, together with biphasic states of the receptive mechanism, are sufficient to produce coherent reactions on the reflex levels. Here all functions are simple, but at the same time highly organised. The response is rigidly predetermined within certain limits; there is little choice, and the answer is physiologically inevitable. In strict accordance with such an arrangement,

we find that the first sorting of afferent impulses within the spinal cord is concerned mainly with their redistribution according to quality. Those capable of exciting pain are gathered together, whatever their peripheral origin, and all those which can evoke sensations of heat or of cold are combined in two specific groups.

After the multitudinous impulses produced by the impact of external and internal forces on the organism have carried out their reflex and co-ordinating functions, the remainder may pass on to excite sensations. These form an essential element in conscious acts, and here the rigidity of response, so characteristic of reflex activity, would be disastrous. The limited freedom of the lower levels must be expanded, so that the physiological reaction may become less inevitable and more elastic.

Moreover, the sensations to which these impulses can give rise are frequently incompatible; a temperature of about 45° C. stimulates at one and the same time organs capable of evoking pleasant heat, cold, and pain. These sensory and affective states cannot co-exist in consciousness; the struggle between the diverse groups of afferent impulses takes place, therefore, on the physiological level, and the victor alone appears as a sensation.

The simplest sensory act is the result, not only of prolonged qualitative integration, but of a constant struggle for physiological dominance. Under normal conditions the result may be inevitable; but there are many cases especially within the visceral field, where no general rule can be laid down, and the response depends on the patient's idiosyncrasy or general resistance. Moreover, his usual reaction may become changed in consequence of some functional alteration in the activity of the central nervous system; impulses may then excite sensation, which normally would have remained outside consciousness.

The following observation, made on my hand in the later stages of regeneration, reveals the struggle for dominance amongst the various afferent impulses excited by thermal stimulation. The dorsal portion of my thumb had so far recovered that contact with a large vessel containing water at 40° C., produced a pleasant well localised sensation of warmth. But, at the same time, the skin in the neighbourhood of the index knuckle was in a pure condition of primitive sensibility, and a cold tube applied to this area evoked a diffuse and vivid outburst of cold referred to the back of the thumb. It was, therefore, possible to stimulate the skin of the thumb with heat, and simultaneously to evoke a sensation of cold referred to the same area. As soon as this was brought about all sensations of heat and cold ceased in the thumb and were replaced by discomfort and pain. When, however, the cold tube was removed

from the neighbourhood of the index knuckle, the direct effect of the hot stimulus in contact with the thumb reasserted itself as pleasant warmth and the pain disappeared.

The behaviour of the normal glans penis ([9], p. 274) forms another excellent illustration of such inhibition. It is not uncommon to find that the punctate end-organs with which it is endowed are not uniformly distributed; the tip of the glans around the meatus may be devoid of heat-spots, but sensitive to cold and to pain. In such a case we carried out the following remarkable experiment. The end of the penis was dipped into a glass containing water at 40° C.; since no heat-spots were present and this temperature has no effect upon the cold-spots, the only sensation evoked was a peculiarly disagreeable pain. When, however, the temperature of the water was raised to 45° C., pain was to a great extent displaced by a vivid sensation of cold, due to stimulation of the cold-spots. Instead of increasing the discomfort an elevation of temperature ceased to be strictly painful because of the appearance of the specific sensation of "paradox cold." But around the corona the penis is always well furnished with heat-spots in addition to those for cold and for pain; as soon then as the water at 45° C. covered the corona without reaching the foreskin, both cold and pain disappeared, giving place to an exquisitely pleasant sensation of heat.

In none of these cases was the process of selective inhibition in any way conscious. The sensation evoked was a definite one of heat, of cold, or of pain; but it was the final issue of a struggle between incompatible and mutually antagonistic afferent impulses. The whole process takes place on the physiological level, and would have remained incomprehensible, had it not been for our knowledge of the phenomena of sensory dissociation.

Many impulses capable of forming the basis of a sensation are prevented under normal circumstances from reaching the highest centres; or, if their forward path is not completely barred, they pass on in a profoundly modified form, in consequence of the concurrent activity of other sensory end-organs. The utility of this arrangement is obvious, especially with those impulses which underlie discomfort or pain.

Pain is the oldest defensive reaction and potentially unpleasant stimuli are the basis of most primitive reflexes. It is, therefore, most important that the impulses they evoke should be diminished in extent, or actually inhibited in favour of those sensory impressions more capable of leading to discriminative action. The mechanism underlying the production of pain and discomfort must, however, remain in full physiological activity, so that it can play its part in defence of the organism, when noxious stimuli reach a high grade of intensity.

Thus, afferent impulses from the viscera do not normally enter consciousness. The eupeptic knows nothing of the processes of digestion beyond a certain gentle sense of well-being. But under abnormal conditions afferent impressions from the internal organs are capable of arousing pain and discomfort. These parts are probably innervated, like the glans penis, from the deep and protopathic systems; but unlike the glans their sensibility is extremely low. All power of conscious response to heat and cold is certainly absent from the greater part of the stomach and intestines, and pain cannot be produced by burning, cutting, and the prick of a pin or other sharp instrument. Internal surfaces are unable to respond to artificial stimuli to which they have never been exposed during the life of the individual or the race. But the hollow viscera, such as the stomach and bladder, react briskly to changes in tension which are their natural mode of stimulation.

Even if a stimulus is capable of exciting these sheltered parts of defective sensibility, it does not usually produce a sensation on account of the resistance of the nervous system to such potentially painful impressions. But a sensory response may be evoked whenever these visceral impulses become sufficiently strong to overcome the inhibition, or the forces opposing their passage are in any way diminished. Once the path has been opened and the dominance of the higher reflexes overcome, a weaker visceral stimulus will be followed by sensation; to this diminished resistance is due the production of pain from otherwise inadequate causes, where visceral irritation has been long continued.

Thus, under favourable conditions, afferent impulses from the viscera are capable of arousing pain and discomfort. But this does not of necessity point to the part diseased; the pain may be a manifestation of abnormal activity on the part of healthy organs, to which they have been excited by a morbid process elsewhere. In the earlier stages of inflammation of the appendix or with affections of the gall-bladder, the pain may be due to abnormal movements of the stomach and intestine; under such conditions it expresses the response of normal parts to a lesion situated in some allied physiological system.

Now we have reason to believe that the viscera have a double afferent supply ([9], p. 64). One of these corresponds to that deep system, which in the limbs supplies muscles, tendons and joints, and remains intact, when all cutaneous nerves are severed ([9], p. 246). This gives rise to Sherrington's proprioceptive reflexes, that have so profound an influence on the regulation of posture and movement. The peculiar aptitude possessed by a part innervated from this deep afferent mechanism, is the power of responding

to stimuli, which produce alterations in form or pressure.* Excessive tension may evoke pain, and "cramp" is the response of these end-organs to abnormal muscular contractions. Parts innervated in this manner are insensitive to light contacts, pricking, heat and cold; but they are so endowed with definite local signature, and the patient is capable of appreciating within certain limits the site of the stimulated spot. It is this system which is responsible, not only for the muscular pains of intestinal colic, but also for the local pain and tenderness on pressure, associated with inflammation of the serous membranes, such as the pericardium, pleura and peritoneum. In fact, these cavities behave like the inner surface of joints ([4], p. 93 and [6], pp. 157 and 232).

But the internal organs are also supplied from another neural system, equivalent, we believe, to the cutaneous punctate mechanism. Even in the skin, the pain-spots are far more numerous than those for heat and cold; protopathic sensibility is essentially a warning mechanism, and most of the viscera, excepting the œsophagus and bladder, seem to be devoid of all sensory response to purely thermal stimulation, as might have been expected from their sheltered position.

One of the most striking characters of pain, or indeed of any sensation, evoked from my hand in a protopathic condition, was its tendency to be referred into remote parts. Portions of the skin seemed to be linked up together in a peculiar manner, so that a stimulus applied to the one produced a diffuse outburst localised in the other. When pain of this order has been aroused in the visceral system, the sensation may be referred to the surface of the body, which becomes tender to cutaneous stimulation. This is not a "hyperalgesia," but a tendency to react more vividly to any excitation capable of evoking discomfort. The threshold to pricking is not lowered, but the vehemence of the response, both sensory and reflex, is greatly increased.

Now this over-reaction is associated with reflexes which still reveal their old impulsive character. The abdominal muscles become tonically contracted, and the leg is drawn up on the affected side. The sufferer is forced

* Afferent impulses, due to changes in the volume of the lungs, belong to this deep or proprioceptive group [3]. They give rise to the Hering-Breuer reflex; inflation produces an expiratory effect, whilst diminution in volume acts as an inspiratory stimulus. I was able to show that this did not depend on the absolute, but on the relative size of the lung; thus the same volume might produce either an inspiratory or an expiratory effect, according to whether it was reached by allowing the lung to collapse or by increasing its content. Moreover, such stimuli evoke a strong negative after-action in the respiratory centre, so that long continuance of one form of stimulation favours response to its opponent; they exhibit, in fact, a remarkable example of biphasic activity.

to creep into some sheltered place, and to lie curled up until he either dies or recovers. All capacity to move the body as a whole is abolished; the reactions of the part affected now dominate the activity of the complete animal. Visceral reflexes of this order are antagonistic to general movements, and this is expressed not only in muscular immobility but in the mental attitude which accompanies visceral pain ([7], p. 373).

Referred pain of visceral origin and the tenderness which accompanies it may be confined to the territory of a few segments only, representing the nerve supply of the affected organ. But if the stimulus is extremely severe, as, for example, during an attack of gall-stone or renal colic, the pain may spread widely even in otherwise normal persons. Not only does it become bilateral, but it is liable to extend both upwards and downwards into regions that stand in no direct nervous relation with the affected organ ([4], p. 104).

Should a referred pain become chronic, this forms an even more important cause for its diffusion. It tends to spread by the fact of its duration. For not only is the general resistance of the patient worn down by the disease, but the passage of painful impulses is facilitated by time.

Certain segmental areas seem to be related to one another, although they are situated far apart on the body. Organs such as the uterus and the breast stand in a close mutual connexion, and within twelve hours of labour, referred pains not uncommonly appear in the front of the chest and in the scapular regions; these come and go with the "after pains," and can be increased by the action of ergot or by manipulating the uterus.

These phenomena of "generalisation" or "spread" of visceral pain and tenderness are of such common occurrence that they form an important factor in the clinical picture of many diseases ([4], p. 105). Diffusion of painful sensations is due to diminished central resistance; potentially painful impulses are allowed to spread widely, which would normally have been inhibited or strictly confined to areas appropriate to the organ affected.

The general bodily state associated with menstruation forms one of the most potent causes of diminished automatic control. This physiological act may be accompanied by referred pain, confined strictly to those segments which stand in direct relation with the pelvic organs; or the morbid sensations may occupy the whole of the body and lower extremities below the level of the umbilicus, with or without the cervical areas and occipital region of the scalp. Finally, the head, trunk, and even the limbs may become painful and tender in parts that have no direct relation to stimuli within the pelvic organs. The extent to which such widespread generalisation

occurs, depends more on the temperamental condition of the patient than on the intensity of the painful irritation.

A sudden rise of temperature is also a frequent cause of "generalisation" of pain. Follicular tonsillitis or any parenchymatous affection of the tonsils may be directly associated with superficial tenderness on the same side, extending from the lower part of the mastoid almost to the middle line in front: the so-called "hyoid" area. Suppose, however, that the onset is sudden and is associated with fever, we may now discover pain and tenderness on both sides of the neck, over the forehead, occipital region, and even in the back or other parts of the body and limbs.

Anæmia is another fruitful cause of "generalisation." A patient may be profoundly anæmic, and yet suffer from no pain or tenderness. But, as soon as some source for pain is present, it at once begins to spread. Toothache in an anæmic patient is a diffuse affection, extending far beyond the segmental areas connected in any way with the irritated organ. If the local cause is removed, the pain does not cease, at any rate immediately: for when central resistance has once broken down, control is recovered with difficulty.

In all such cases, the pain originated in some definite and recognisable cause; it spreads widely because of the severity or long duration of the stimulus, or in consequence of the relaxation of central control, which may accompany menstruation, pyrexia, or anæmia. But sometimes pain and tenderness of this order may become widely diffused in consequence of some debilitating psychological state, such as anxiety or emotional shock. Neuralgia and superficial tenderness of dental origin not uncommonly assume undue proportions owing to insomnia and worry, and the mental state of the patient has a profound influence over pains originating in the pelvic viscera.

Occasionally the central resistance to potentially disagreeable impulses is temperamentally so low that pain may appear without any obvious cause for peripheral irritation. Some women are rarely free from tender spots in various parts of the body, representing the maxima of one or more of these tender areas; they form foci from which pain may generalise widely under the influence of emotion or other conditions which lessen the dominant power of higher centres. No gross visceral stimulus is required; the central apparatus is already in an explosive condition, and any relaxation of physiological control leads to an outburst of energy manifested in widespread discomfort. In such cases the order in which the phenomena appear does not follow the rules that can be laid down for pain of visceral origin. Severe pain over the lower part of the abdomen and back may be accompanied by headache and tenderness situated over the forehead; the trunk can be widely affected without the head and neck or *vice versa*. Such want of harmonious

correlation points to the central origin of these morbid phenomena ; they are not the direct expression, however extensive, of peripheral stimulation.

Pain and discomfort are the motive force of most elementary reflexes ; any stimulus capable of exciting disagreeable effects is naturally shunned, and the organism tends to turn towards those which are pleasurable. But such protective reactions permit of little choice and they must be controlled on the physiological level in favour of more discriminative responses ; for without such re-adjustment functional development would be impossible. Moreover, in order to acquire some new facility, it may be necessary to inhibit even normal sensory responses, which, from their disagreeable nature, are intended to compel us to avoid the conditions that evoke them.

For instance, all healthy persons can be made giddy, provided the rotatory movement is sufficiently violent, especially if the head is held in some unusual position. This reaction, even when it culminates in vomiting, is not a pathological condition ; it is the normal response to an acute disturbance of equilibrium. A similar vertigo can sometimes be produced by visual impressions, without any change in bodily posture. But the ease with which these unpleasant states can be evoked differs within wide limits in individual cases and varies greatly at different times. Some, who in childhood were unable to swing without discomfort and were sick on a train-journey, cease to suffer in adult life, and, provided the stimulus is not unusually severe, differ little in their reactions from their fellows.

Even in the fully developed nervous system of man, the acquisition of some new aptitude is associated with increasing control over sensory impressions ; we learn to adapt ourselves to the conditions around us, and cease to be the victims of uncoordinated reactions. This is particularly evident when learning to fly, for many normal men become giddy, and even vomit on exposure to rapid changes of posture in the air ; but the majority quickly recover, and may become expert and bold aviators. They have adapted themselves to the new conditions ; the stimuli from the peripheral end-organs no longer dominate the field of response. They are controlled or suppressed, not by the will, but by that power of adaptation which is one of the most potent automatic factors in the activity of the central nervous system ([8], p. 13).

Anything which diminishes this physiological efficiency tends to lessen control over the reaction of the lower centres to sensory stimulation. A gastro-intestinal attack, influenza, an aeroplane accident, domestic worry, or fear, will all act in the same direction. A man, who was giddy when he first went into the air but recovered completely, may fall back to his original mode of reaction, and become unable to carry out any aerobatic

evolution, whilst one who has never experienced any previous discomfort may develop undue susceptibility to rotatory stimuli. Such persons are no longer normal, not because the response is a pathological one, but because for a time, at any rate, they have been reduced to a lower level of functional efficiency.

If we responded constantly and inevitably to all impulses from peripheral end-organs, we should be automata, the victims of indiscriminate reactions. But, with the gradual evolution of its functions, the central nervous system acquires ever increasing control over afferent impressions produced by the action of external forces. Such development takes place not only in the race, but in the life of the individual; and it is to this that we owe our power of acquiring new reactions and facilities.

During this evolution of function, the power of responding in a more primitive manner is not lost. The mechanism of the older and more immediate reaction remains intact; but its activity is held in check, ready to become manifest should the noxious stimulus become unduly intense. All normal persons become giddy if a rotatory stimulus is sufficiently severe, or if it comes into action suddenly, especially if it is greater in one ear than in the other. In the same way, everyone, however healthy, is liable to suffer from pain during the passage of a renal calculus.

But in states of disease this automatic control is likely to break down, less from the violence of the stimulus than from causes which lower physiological vitality. Of these, infective and toxæmic states are often potent on the physical side. Psychical conditions, especially those associated with neural exhaustion, whether temperamental or acquired, may also lead to profound loss of capacity to dominate impulses derived from peripheral stimulation.

Conclusions.

(1) Hughlings Jackson laid down the rule that destructive lesions do not cause positive effects, but induce a negative condition, which permits positive symptoms to appear. I have attempted to apply this law to a number of cases where organic destruction of some part of the nervous system is followed, not only by loss of function, but by some form of over-activity.

(2) Such abnormal reactions cannot be attributed to "irritation." It must not be supposed that we deny the occurrence of true irritative phenomena. These can be studied most easily in cases of injury to peripheral nerves, where they form an instructive contrast to the manifestations of protopathic sensibility. The pain and tenderness, due to definite irritation of nerve-fibres, occupy the whole territory supplied by the affected trunk; but a comparatively small number of the conditions which follow a destructive

lesion can be attributed to this cause. On the other hand, protopathic sensibility is extremely common and occurs solely over parts where finer sensory discrimination is defective. Trotter [19] has put forward the theory that these peculiarities of response are due to exposure of the constituent elements of the closed nervous system to the irritative effect of contact with somatic tissues. Even this view will not explain the abnormally vivid pleasure which may constitute one of the factors in protopathic over-response. It does not help us to understand the peculiar form assumed by the sensibility of the normal glans penis. Nor can it account for the transitory regression and recovery in the sensory condition of my hand during the second stage of recovery after exposure to the injurious effects of cold. The vividness of response and reference into remote parts returned; but they disappeared again when the sensibility of the hand was restored by warmth.

No one has attempted to apply this conception of the irritative effect of contact with somatic tissues to the phenomena of thalamic over-reaction or to other analogous conditions. On the other hand, we have tried to explain such manifestations of over-activity, whether motor or sensory, due to a purely destructive lesion of the nervous system, by the general law of release of subordinate functions.

(3) The conception of levels of activity within the nervous system was one of the fundamental aspects of Hughlings Jackson's teaching. To him a "level" was always one of function rather than of structure. So, whenever I have spoken of higher and lower centres, these must be considered as nodal points of neural activity, and not of necessity as anatomical structures. In the illustrations, chosen to support my thesis, they were anatomically separable; for otherwise it would have been impossible to prove my contention, that removal of a dominant activity, was responsible for the phenomena under investigation.

(4) Removal of a dominant neural mechanism permits the activity of lower centres to appear. These unfettered manifestations are not fortuitous pathological states, but represent that part of a complex reaction, which still remains active; they display characters more primitive than those of the complete functions in which they normally play a part. The response is massive and of unusual extent and vigour; on the motor side it may affect organs which do not normally lie within its reflex arc. Such stereotyped reactions can be excited indifferently from an unusually wide field. They are impulsive and assume the form of a warning or defensive response, regulated more definitely by the extent than by the degree of intensity of the stimulus.

But release from control due to a destructive lesion does not reveal such lower activities in all their original simplicity; for in most cases they have

been profoundly modified by the advent of the new centres, which utilise and develop some of the functions originally possessed by the older mechanism.

(5) This dominance of higher over lower forms of neural activity is the consequence of integration within the central nervous system; it is carried out partly by qualitative selection, but to an even greater extent by the struggle for expression between incompatible physiological reactions. This involves permanent inhibition, under normal conditions, of one group of processes, or temporary suppression of these primitive activities until the need should arise for a more impulsive mode of response.

(6) All newly acquired abilities depend on a fresh adjustment of co-ordinated reflexes, and even certain responses from normal sense-organs may be suppressed or held in check. This demands the exercise of permanent physiological control, which may break down under certain conditions, and permit the dominated function to express itself unchecked. A stimulus of excessive vehemence or prolonged duration, any abnormal state which lowers the vitality of the nervous system, and even some inherent want of resistance may all lead to unexpectedly disagreeable and impulsive reactions.

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*Preliminary Report of the Mackie Ethnological Expedition to
Central Africa.*

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[PLATES 12-16.]

At the outset I realised it would be impossible to find the right men in England to join the expedition, owing, firstly, to the fact that the men whom I should have liked to accompany me were only then returning from France, and secondly, because of the expense. I therefore set out alone, hoping to find at least a photographer and a typist either in Mombasa or in Uganda.

At Mombasa it was impossible to find any man suitable for my purposes, so I journeyed on to Nairobi and spent a week there seeking men; but here again failure forced me to go on to Uganda. In Uganda I thought I was securing the men I required, but I soon discovered they were not suited to my purpose and had to be dismissed.

In Uganda a month was spent at Kampala making enquiries into some of my past work and correcting some things in my former book on the Baganda. There were also men to be interviewed and engaged; but, over and above these matters, I was entrusted by the Government with the task of looking into some native questions which called for attention. I was engaged investigating native secret societies during the whole of the expedition, and it was only at quite the end of the time that I was able to give a satisfactory account of them to the Government authorities.